



Potential impacts of a future persistent El Niño or La Niña on three subspecies of Australian butterflies

Linda J. Beaumont^{1,3}, Daisy Duursma¹, Darrell J. Kemp¹, Peter D. Wilson¹, and Jason P. Evans²

¹ Department of Biological Sciences, Macquarie University, NSW 2109, Australia

² Climate Change Research Centre and ARC Centre of Excellence for Climate System Science, University of New South Wales, Randwick, NSW 2052, Australia

ABSTRACT

One of the major uncertainties of 21st century climate change is the potential for shifts to the intensity and frequency of the El Niño Southern Oscillation (ENSO) cycle. Although this phenomenon is known to have dramatic impacts on ecosystems regionally and globally, the biological consequences of climate change-driven shifts in future ENSO events have been unexplored. Here, we investigate the potential impacts that a persistent El Niño, La Niña, or ‘Neutral’ phase may have on species distributions. Using MaxEnt, we model the distribution of climatically suitable habitat for three northeast Australian butterfly subspecies (*Doleschallia bisaltide australis*, *Hypolimnas alimena lamina*, and *Mycalis terminus terminus*) across the three ENSO phases. We find that the spatial extent and quality of habitat are lowest under conditions that would characterize a persistent El Niño (hot/dry). In contrast, suitable habitat is broadest under the warm/wet conditions associated with La Niña. Statistical analyses of the difference between pair-wise combinations of suitability maps using Hellinger distance showed that projections for each subspecies and ENSO phase combination were significantly different from other combinations. The resilience of these, and other, butterfly (sub)species to changes in ENSO will be influenced by fluctuations in the strength of these events, availability of refugia, and life-history characteristics. However, the population dynamics of wet- and dry-season phenotypes of *M. t. terminus* and physiological limitations to high temperatures suggest that this subspecies, in particular, may have limited resilience should the strength and frequency of El Niño events increase.

Key words: butterflies; climate change; distributions; ENSO; Hellinger distance; MaxEnt.

THE EL-NIÑO SOUTHERN OSCILLATION (ENSO) HAS SUBSTANTIAL IMPACTS ON ECOSYSTEMS (Holmgren *et al.* 2001, Woodward *et al.* 2008, Ancona *et al.* 2011) through changes in precipitation intensity, distribution and predictability, temperature, and incident radiation. This ocean–atmosphere phenomenon occurs across the tropical Pacific Ocean in pseudo-cycles of 2–7 yr, influencing global climates, ecosystems, and societies (Latif & Keenlyside 2009, Vecchi & Wittenberg 2010). Environmental variables directly and indirectly linked to ENSO can drive the population dynamics of many species (Waite *et al.* 2007, Hewitt & Thrush 2009) and influence ecosystem productivity and carbon sequestration.

The response of tropical ecosystems to ENSO events is apparent in analyses of atmospheric CO₂ growth rates: warmer and drier conditions associated with El Niño can increase fire events and reduce ecosystem productivity, thereby increasing atmospheric CO₂ growth rates (Patra *et al.* 2005). Conversely, cooler, wetter conditions associated with La Niña enhance productivity and provide a greater CO₂ sink (Patra *et al.* 2005) with plant growth in southern Africa and Central Asia, in particular, being strongly driven by ENSO cycles (Potter *et al.* 2008).

Precipitation is a core driver of productivity in arid and semi-arid regions. Increase in rainfall resulting from ENSO

events is critical for primary productivity and the diversity of these ecosystems (Holmgren *et al.* 2006). In these regions, pulses in primary productivity resulting from higher rainfall lead to greater herbivore abundance with flow-on effects through the food web, while ENSO-associated droughts can cause emigration or population crashes (Holmgren *et al.* 2006). ENSO events have also been shown to trigger insect (Paritsis & Veblen 2011) and disease (Anyamba *et al.* 2012) outbreaks.

ENSO AND CLIMATE CHANGE

The last millennium has seen periods of stronger (*e.g.*, the mid-1600s) and weaker (*e.g.*, 1400s) ENSO activity, with decadal-scale changes occurring throughout the 20th century (Latif & Keenlyside 2009). For example, during the 1950s–1960s, ENSO was relatively inactive, while since the mid-1970s, ENSO activity appears to have increased (Vecchi & Wittenberg 2010). Whether or not the late 20th-century increase in activity was driven by greenhouse gas (GHG) emissions is unclear (Latif & Keenlyside 2009). However, given that inter-annual variation in ENSO is controlled by a balance of amplifying and damping feedbacks, and that climate change will modify at least some of the physical processes governing ENSO (Collins *et al.* 2010), it is likely that the dynamics of ENSO will change in the future. But, how sensitive ENSO is to GHG increases is uncertain (Vecchi &

Received 23 November 2015; revision accepted 2 May 2016.

³Corresponding author; e-mail: linda.beaumont@mq.edu.au

Wittenberg 2010). Global Climate Models (GCM) mostly show that El Niño events will continue to occur throughout the 21st century (Merryfield 2006, Vecchi & Soden 2007, Latif & Keenlyside 2009, Collins *et al.* 2010, Vecchi & Wittenberg 2010). Furthermore, recent modeling suggests that the frequency of extreme ENSO events may double from approximately one event per 20 yr to one event per 10 yr (Cai *et al.* 2014, 2015). Unfortunately, robust assessments of future activity of this phenomenon cannot yet be made (Vecchi & Soden 2007, Latif & Keenlyside 2009, Collins *et al.* 2010, Vecchi & Wittenberg 2010). It is worth noting, however, that persistent El Niño-like conditions have existed previously (*e.g.*, during the Pliocene warm period ~4.5–3 million yr BP, and which was the last time global temperatures were warmer than today) (Wara *et al.* 2005). Further, greater variability and intensity of ENSO ~4000 through to 1500 yr BP drove the collapse of coral reefs in the Eastern Pacific (Toth *et al.* 2012). Given that ENSO has a significant impact on the biosphere, future changes in the intensity and frequency of these events may have serious ecological and societal ramifications (Latif & Keenlyside 2009).

In this study, we use MaxEnt (Phillips *et al.* 2006), a species distribution model (SDM), to assess the potential impact that future persistent El Niño, La Niña, or Neutral conditions may have on the distributions of three subspecies of Nymphalid butterflies (*Dolerichthys bisaltide australis*, *Hypolimnastis alimena lamina*, and *Mycalopsis terminus terminus*) found across Northern Australia. All three subspecies exhibit marked reproductive seasonality, with recruitment into each successive breeding season critically dependent on the ability of individuals to survive the intervening (dry-season) periods of adversity, with seasonal polyphenism (wet-season vs. dry-season forms) apparent in *M. t. terminus*. As such, anomalous ENSO-driven temperature and precipitation changes may affect population sizes. This is supported by evidence that ENSO events can have direct impacts on butterfly abundance and condition (Vandenbosch 2003, Srygley *et al.* 2010), as well as indirect impacts through ENSO-driven disturbances such as fire (Cleary & Grill 2004, Charrette *et al.* 2006).

METHODS

STUDY SPECIES.—The three butterfly species each have one subspecies that is common and widespread in northeastern Australia and the Torres Strait. While *D. b. australis* and *H. a. lamina* occupy lowland rain forests (the habitat of their primary endemic host-plant, *Pseuderanthemum variable*, Acanthaceae), *M. t. terminus* is found in a variety of habitats where it prefers moist, shaded areas (Braby 2004). This species exhibits a marked seasonal polyphenism, with wet and dry season forms expressing significant differences in body size and phenotypic wing characters such as eyespots (Braby 1994a). Adults of *M. t. terminus* are most abundant during the early dry season, and while breeding occurs over most of the year, egg production declines with the progression of the dry season (*i.e.*, from early April through late September). Toward the end of the dry season, females may exist in a state of

reproductive diapause (Braby 1994a, 1995). In contrast, adult *D. b. australis* and *H. a. lamina* are more abundant throughout the wet season, with reproduction closely tied to localized patterns of rainfall and host-plant growth (Braby 2004). During dry-season months, adults of both species occur in close association at the same overwintering sites as their relative *Hypolimnastis bolina* (Kemp 2001). As with the better-documented *H. bolina* (Kemp 2001, Pieloor & Seymour 2001), these subspecies are likely to undergo a regularly timed adult diapause to ‘escape in time’ during the dry-season months unfavorable for reproduction.

SPECIES DATA.—We obtained occurrence records for the subspecies from the Dunn and Dunn National Database of Australian Butterflies (Dunn & Dunn 2006). The data base is a compilation of records from public and private natural history collections across Australia and the literature. For each subspecies, we collated records dated December, January, February, or March and which: (1) were from January 1911 onwards; (2) gave the year of the collection or observation; and (3) had latitude and longitude recorded. This resulted in 126 records for *M. t. terminus*, 93 for *H. a. lamina*, and 69 for *D. b. australis*. We ensured that records for each species spanned ENSO events that were classified as Neutral, El Niño, and La Niña. Finally, background points, necessary for the species distribution models, were generated from all butterfly occurrence records for the months of December through March in the Dunn and Dunn Database, which were within 200 km of the subspecies’ distributions.

We restricted occurrence records to the December–March period in order to assay each species during the first half of its annual breeding season. This approach was designed to capture annual variation in the recruitment of populations from the dry season immediately preceding the occurrence record and to provide the cleanest possible signature for testing the effects of Neutral, El Niño, and La Niña conditions.

CLIMATE DATA FOR ENSO PHASES.—Monthly data for minimum and maximum surface temperature (T_{\min} , T_{\max}) and precipitation (Pr) from January 1910 onwards were obtained from the Australian Bureau of Meteorology, at a resolution of 0.05° latitude and longitude (Jones *et al.* 2009). Each month was classified as Neutral, El Niño, or La Niña, based on the standardized Southern Oscillation Index (SOI). Following Trenberth (1984), this was calculated by subtracting the standardized Darwin sea level pressure (SLP) from the standardized Tahiti SLP (standardized using the standard deviation of their monthly values over the period 1951–1980). Darwin and Tahiti SLP and SOIs were obtained from NCEP (<http://www.cpc.ncep.noaa.gov/data/indices/>), with data prior to 1935 added from the Climate Research Unit (<http://www.cru.uea.ac.uk>). Months with values > 1 Pa/Pa were classified as La Niña, those with <–1 Pa/Pa were El Niño, and months with values in between were ‘Neutral’.

We created 10 climate datasets for each ENSO phase (Neutral, El Niño, La Niña) by randomly sampling from all Neutral

(or El Niño or La Niña) months from 1911 to 2010. For example, 10 Neutral Januarys were selected randomly from all Januarys classified as Neutral, 10 Neutral Februarys were selected randomly from all Februarys classified as Neutral, and so on for March–December. The 10 sets of climate data were necessary to obtain a statistical sample of the different ENSO phases, given the relatively large natural variability within each phase, and to ensure that constructed ENSO phases had the correct weather/climate statistical properties.

For each of the ten versions of climate data for the three ENSO phases (*i.e.*, $N = 30$), we then generated seven bioclimatic variables using the R package ‘dismo’ 0.1–11 (Hijmans *et al.* 2011) (*i.e.*, Seasonal Mean Temperature [SMT], where ‘seasonal’ refers to December–March]; Maximum Temperature of Hottest Month [MTHM]; Mean Temperature of Wettest Month [MTWM]; Total Precipitation [TP]; Precipitation Seasonality (Coefficient of Variation) [PS]; Precipitation of Hottest Month [PHM]; Precipitation of Coldest Month [PCM]) (Table 1). We also calculated a ninth variable, Mean Seasonal Aridity [MSA], using the monthly ratio of actual total evaporation to potential evaporation derived from the Australian Water Availability Project climatologies (<http://www.csiro.au/awap/>).

SPECIES DISTRIBUTION MODELS.—MaxEnt (v. 3.2.3k) (Phillips & Dudik 2008), driven by the ‘dismo’ package (Hijmans *et al.* 2011) in R x64 v. 3.0.1 (R Core Team 2013), was used to model the distribution of climatically suitable habitat for each subspecies. This model is particularly suited to presence-only data and performs well compared with other available species distribution models (SDMs) (Elith *et al.* 2006). Based on the maximum entropy principle, MaxEnt produces a continuous probability field that can be interpreted as a relative index of climatic suitability. Locations with higher values are deemed to have greater suitability for the species modeled (Phillips *et al.* 2006, Phillips & Dudik 2008). A detailed description of MaxEnt is given in Elith *et al.* (2011).

TABLE 1. Characteristics of El Niño, La Niña, and Neutral climate datasets for northeastern Australia, for seven climate variables. Values given are averages with standard deviations in brackets. SMT, seasonal mean temperature; MTWM, maximum temperature of hottest month; MTHM, mean temperature of wettest month; TP, total precipitation; PS, precipitation seasonality (coefficient of variation); PHM, precipitation of hottest month; PCM, precipitation of coldest month; and MSA, mean seasonal aridity index. Units are in °C and mm for temperature and precipitation variables, respectively.

	El Niño		La Niña		Neutral	
SMT	14.4	(1.6)	13.3	(1.4)	13.8	(1.5)
TWM	34.9	(3.4)	34.0	(3.2)	34.5	(3.3)
MTHM	5.8	(3.8)	7.3	(4.1)	6.6	(3.9)
TP	25.7	(5.5)	24.4	(5.3)	25.9	(4.4)
PS	9.2	(10.5)	18.8	(14.7)	14.6	(12.3)
PHM	231.4	(192.1)	342.4	(265.4)	280.4	(211.2)
MSA	36.6	(37.2)	74.3	(49.2)	58.8	(44.1)

We undertook several steps to optimize our models, including (1) assessing the effect of different combinations of feature types; (2) altering the regularization coefficient; and (3) comparing the predictive power of different sets of predictor variables (Appendix S1). ENMTools (Warren *et al.* 2010) was used to calculate the Bayesian (BIC) and sample size corrected Akaike Information Criteria (AIC_c) for each model. The most parsimonious model for the three subspecies was the one calibrated using all feature types, a regularization multiplier of 1, and five climate variables: SMT, TP, PHM, PCM, and MSA. We used this configuration to project habitat suitability across the 30 ENSO climate datasets (*i.e.*, 10 versions of each of the three ENSO phases). The performance of the retained model was evaluated using the area under the receiver operating characteristic (ROC) curve (AUC), and the threshold-dependent binomial test of omission (Appendix S1).

To determine whether spatial patterns in projections of climatically suitable habitat differed depending on the ENSO phase, we calculated the Hellinger distance, which is a spatially explicit, grid cell-by-grid cell comparison of pairs of images (Wilson 2011). In our study, this amounts to calculating the difference between each species \times ENSO phase pair-wise combination of suitability maps, using the MaxEnt habitat suitability index as the continuous variables. Exploratory data analysis was undertaken using Principal Coordinates Analysis (PCoA) (Legendre & Legendre 1998) on the Hellinger distance matrix to visualize relationships between the distribution of climatically suitable habitat and ENSO phases. This was computed using the R package ‘labdsv’ (Roberts 2013). For each subspecies, we calculated one-way ANOVAs with ENSO phase as the factor. We also tested the statistical significance of groups of maps via a permutational multivariate analysis of variance (PERMANOVA). This analysis was performed using the function Adonis in the R package ‘vegan’ (Oksanen *et al.* 2013).

RESULTS

Across our study area in northeastern Australia, El Niño events can be characterized as warmer and drier, and hence have a greater aridity index, than La Niña events. Neutral phases lie in between (Table 1).

For the three subspecies, predictive power of the MaxEnt models was better than random (AUC values: random = 0.5; *D. b. australis* = 0.781 ± 0.048 ; *M. t. terminus* = 0.855 ± 0.023 ; *H. a. lamina* = 0.857 ± 0.045). Omission rates using the minimum training threshold were significantly lower than random for all subspecies ($P \leq 0.001$). We note that omission rates were significant to at least $P = 0.01$ for all eleven thresholds reported by MaxEnt for *M. t. terminus* and *H. a. lamina*, and at least $P = 0.04$ for 10 thresholds for *D. b. australis*.

The geographic extent of climatically suitable habitat for each subspecies was broadest when projected onto La Niña conditions and narrowest under El Niño conditions (Fig. 1). Differences in the distribution of climatically suitable habitat, particularly under El Niño versus La Niña, are also apparent from the PCoA plots of Hellinger distance (Fig. 2). A one-way

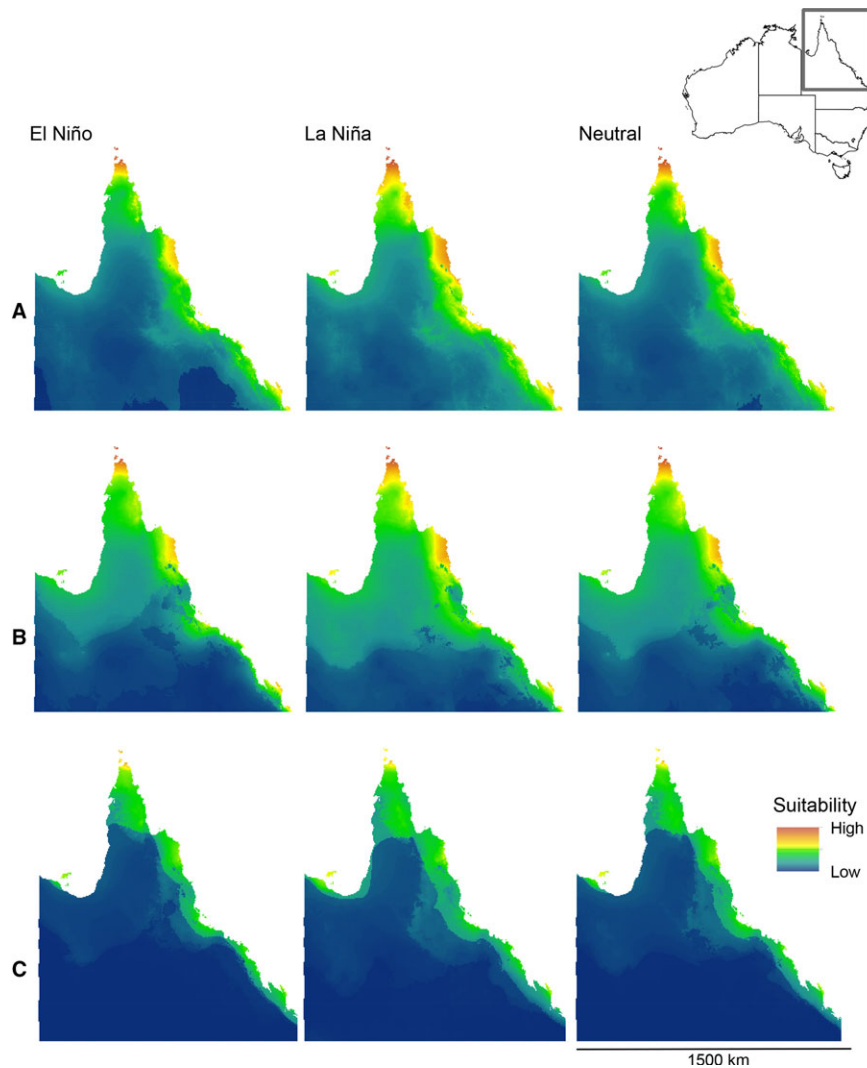


FIGURE 1. MaxEnt projections of climate suitability for three subspecies of Australian butterflies, under persistent El Niño, La Niña, and Neutral phases. (A) *Doleschallia bisaltide australis*, (B) *Hypolimnas alimena lamina*, and (C) *Mycalesis terminus terminus*.

ANOVA for each species (Table 2) confirmed that statistically significant differences occurred in the spatial distribution of suitable habitat across the three ENSO phases ($P < 0.001$). For *M. t. terminus*, ~ 44 percent of variation in the model was explained by the three ENSO phases, whereas this was only 16.8 percent and 10.1 percent for *D. b. australis* and *H. a. lamina*, respectively. For each ENSO phase, MaxEnt models were projected onto 10 climate datasets, and these resulted in significant differences ($P < 0.001$) across maps for *D. b. australis* (38.4%) and *M. t. terminus* (17.5%). A PERMANOVA of species by phases with year nested also gave highly significant P -values (< 0.001) for each factor (Table 3). This result also implies that maps for a given species by ENSO phase combination are distinctly different from other combinations, and that within a combination this trend occurs across the 10 climate datasets.

DISCUSSION

El Niño Southern Oscillation phases can have significant direct and indirect impacts on biodiversity (Hughes 2011). Our models show that the extents of climatically suitable habitat for three subspecies of Australian butterflies contract substantially under the hot/dry conditions that characterize El Niño events, and expand during wetter La Niña events (Fig. 1). It is worth noting that individual ENSO events can differ substantially from one another. The climatologies used for our study, based on the average of 10 randomly selected 20th century events for each ENSO phase, comprise a mix of weaker and stronger events. Given this, future strengthening of either El Niño or La Niña could have greater impacts on species distributions than the results presented here.

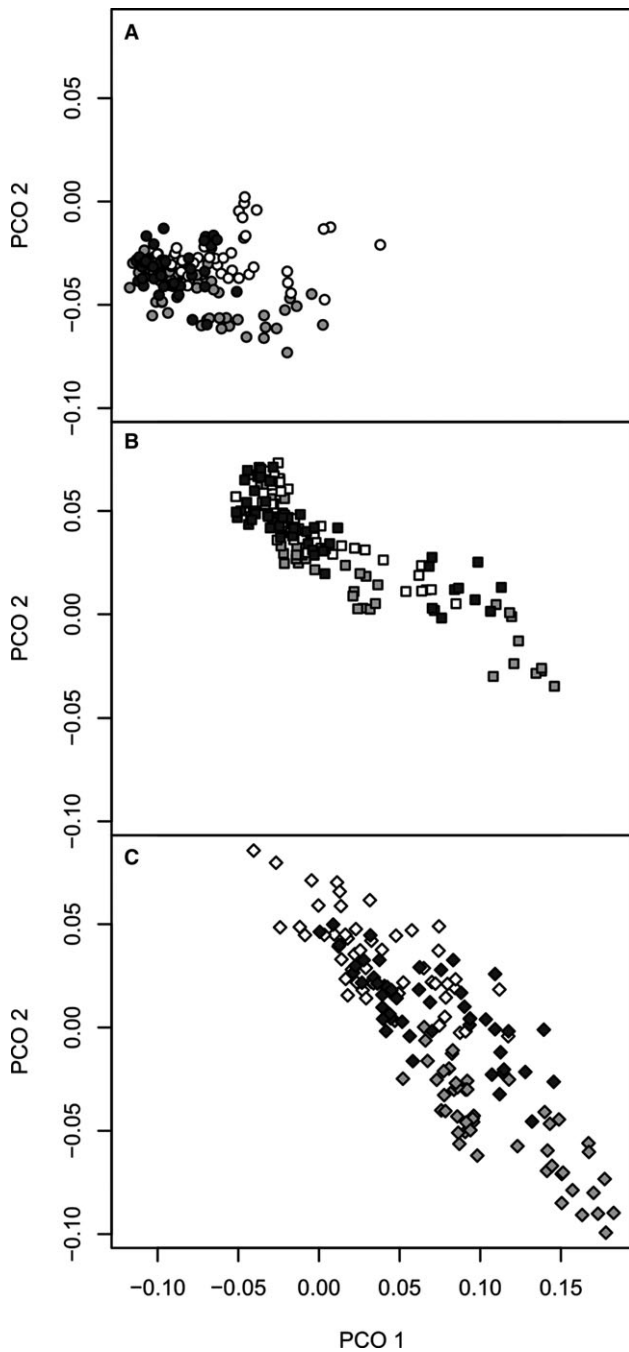


FIGURE 2. Principal Coordinates Analysis of the Hellinger distance matrix. (A) Plot for *Doleschallia bisaltide australis*, (B) *Hypolimnna alimena lamina*, and (C) *Mycalesis terminus terminus*. The first two principal coordinates accounted for 77.1 percent of the variation in spatial distribution of climate suitability. *Doleschallia* was seen to have a different spatial distribution to the other species. However, all species differed in the spatial distribution of climate suitability between the three ENSO phases. El Niño = gray, La Niña = white, Neutral = black symbols

The resilience of butterfly populations to persistent El Niño conditions is unclear but will likely depend on fluctuations in the strength of these events, life history and phenology, and

TABLE 2. One-way ANOVA of Hellinger distance. For three butterfly subspecies (*Doleschallia bisaltide australis*, *Hypolimnna alimena lamina*, and *Mycalesis terminus terminus*), the distribution of climatically suitable habitat differs significantly ($P < 0.05$) across the three ENSO phases (El Niño, La Niña, and Neutral) and, for two subspecies, also among years nested in the model.

Source	df	SS	MS	F	R ²	P
<i>Doleschallia bisaltide australis</i>						
ENSO phase	2	0.063	0.032	22.609	0.17	0.001
ENSO phase [Year]	27	0.143	0.005	3.816	0.38	0.001
Residual	120	0.166	0.001		0.45	
Total	149	0.371			1	
<i>Hypolimnna alimena lamina</i>						
ENSO phase	2	0.061	0.031	7.557	0.1	0.001
ENSO phase [Year]	27	0.059	0.002	0.536	0.1	0.996
Residual	120	0.488	0.004		0.8	
Total	149	0.608			1	
<i>Mycalesis terminus</i>						
ENSO phase	2	0.437	0.218	69.93	0.44	0.001
ENSO phase [Year]	27	0.172	0.006	2.042	0.18	0.001
Residual	120	0.375	0.003		0.38	
Total	149	0.984			1	

TABLE 3. A permutational multivariate analysis of variance (PERMANOVA) of Hellinger distances (species \times phase with nested year) indicated highly significant P-values for each factor. This implies that the distribution of climatically suitable habitat for three subspecies of butterfly and ENSO phase combinations (El Niño, La Niña, and Neutral) are distinctly different from other combinations. Furthermore, within a combination, there is a trend over the 10 sampled years.

Source	df	SS	MS	F	R ²	P
Species	2	2.180	1.090	381.28	0.53	0.001
ENSO phase	2	0.320	0.160	55.96	0.08	0.001
Species:ENSO phase	4	0.241	0.060	21.08	0.06	0.001
Species:ENSO phase [Year]	81	0.374	0.005	1.61	0.09	0.001
Residual	360	1.029	0.003		0.25	
Total	449	4.143			1.00	

availability of refugia. Presently, little is known about how ENSO cycles influence Australian insect populations. For tropical species, population dynamics such as breeding strategies during wet versus dry seasons may help to identify potential responses to a persistent El Niño (or La Niña). For example, although *M. t. terminus* breeds across most of the year, reproductive activity declines as the dry-season progresses and in some locations may cease for short periods in the late dry season (Braby 2002). Laboratory experiments have shown that few eggs of this species

survive temperatures $>30^{\circ}\text{C}$, and none survive temperatures $>35^{\circ}\text{C}$ (Braby & Jones 1994). This suggests that a greater frequency and intensity of El Niño events may have detrimental impacts on the population dynamics of this subspecies. Little is known of the population dynamics of *H. a. lamina* and *D. b. australis*.

ENSO events may indirectly affect butterflies via the responses of host plants to changes in rainfall and solar radiation. In western North America, fluctuations in the abundance of the butterfly species *Vanessa cardui* are strongly coupled to El Niño (Vandenbosch 2003). Above-average winter rainfall associated with these events enables greater plant productivity, which in turn supports irruptions of this species (Vandenbosch 2003). Similarly, the timing of migration of the butterfly *Aphrissa statira* across the Panama Canal is influenced by ENSO and begins approximately 4 wk after the start of the wet season (Srygley *et al.* 2010). However, in the wet forests of this region, lianas on which *Aphrissa* feed respond positively to higher SST and reduced rainfall, characteristic of El Niño years, with greater leaf flushing, enabling higher butterfly numbers (Srygley *et al.* 2014).

ENSO events are also likely to influence the growth regimes of larval host plants, thereby exerting indirect effects upon butterfly populations. This could arise via changes in the quality and/or availability of host-plant foliage. Larvae of the three subspecies in our study feed on several native and introduced grasses or herbs. As the dry season progresses, the quality of host plants declines and some grasses may die off (Braby 1995). Larvae from larger *M.t. terminus* eggs have a significantly higher survival rate when reared on tough, nitrogen-poor leaves than larvae from smaller eggs: in contrast, large egg size does not confer an advantage when larvae feed on high-quality leaves (Braby 1994b). Where present, variation in key traits such as egg size (which primarily determines the head capsule size of larval hatchlings) may buffer at least shorter-term changes in host-plant quality. If such variation has a genetic basis, as demonstrated for African *Bicyclus* (Fischer *et al.* 2004), then evolutionary adaptation (Hoffmann & Sgro 2011) is also a possible response to persistent El Niño states.

A potentially more significant outcome is that ENSO events could lead to reduced availability of host-plant foliage *per se*. This holds particularly for species that depend on annual hosts, such as *Mycaliesis spp.*, or which otherwise possess reproductive strategies precisely timed to coincide with plant growth periods (*e.g.*, *Hypolimnas*; Kemp 2001). Tropical Australian butterflies exhibit notable variation in how they deal with seasonal adversity, spanning strategies of ‘escape in space’ (*e.g.*, continuous breeding in refugia and/or migration) to ‘escape in time’ (*e.g.*, estivation and true reproductive diapause; Jones 1987, Jones & Rienks 1987, Braby 1995). Whereas migration and estivation allow a measure of flexibility, diapause is programmed according to the environmental cues that have historically predicted the onset and cessation of favorable breeding conditions (Jones & Rienks 1987). Often these same cues directly mediate host-plant growth. Where cues vary between butterfly and plant, however, a relatively rapid change in climatic regimes could result in diapause schedules that

are increasingly displaced from resource availability. Adaptive potential (in both butterflies and their hosts) may again be informed by knowledge of phenotypic plasticity and genetic variation (Hoffmann & Sgro 2011). Evidence of a recent shift in the timing of adult emergence in the temperate Australian satyrine *Heteronympha merope* (Kearney *et al.* 2010) supports close consideration of breeding phenology in future work.

At present, the intensity and frequency of future El Niño events is uncertain (Merryfield 2006, Latif & Keenlyside 2009, Collins *et al.* 2010, Vecchi & Wittenberg 2010). Regardless, even in the absence of significant changes to future ENSO cycles, projected drying of the Australian continent over the 21st century will enhance the impacts of El Niño and dampen the impacts of La Niña events (Vecchi & Wittenberg 2010). A greater understanding of species responses to ENSO events could play a substantial role in predicting biological consequences of 21st-century climate change (CSIRO & BoM 2007).

ACKNOWLEDGMENTS

We thank Robert Srygley and anonymous reviewers for invaluable comments on a previous version of this article. We also thank the many collectors who have recorded butterfly occurrences over the years.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. Model selection and evaluation.

LITERATURE CITED

- ANCONA, S., S. SANCHEZ-COLON, C. RODRIGUEZ, AND H. DRUMMOND. 2011. El Niño in the Warm Tropics: Local sea temperature predicts breeding parameters and growth of blue-footed boobies. *J. Anim. Ecol.* 80: 799–808.
- ANYAMBA, A., K. J. LINTHICUM, J. L. SMALL, K. M. COLLINS, C. J. TUCKER, E. W. PAK, S. C. BRITCH, J. R. EASTMAN, J. E. PINZON, AND K. L. RUSSELL. 2012. Climate teleconnections and recent patterns of human and animal disease outbreaks. *PLoS Negl. Trop. Dis.* 6: e1465.
- BRABY, M. 1994a. Phenotypic variation in adult *Mycaliesis* Hubner (Lepidoptera: Nymphalidae: Satyrinae) from the Australian wet-dry tropics. *J. Austral. Entomol. Soc.* 33: 327–336.
- BRABY, M. 1994b. The significance of egg size variation in butterflies in relation to hostplant quality. *Oikos* 71: 119–129.
- BRABY, M. 1995. Reproductive seasonality in tropical satyrine butterflies: Strategies for the dry season. *Ecol. Entomol.* 20: 5–17.
- BRABY, M. F. 2002. Life history strategies and habitat templates of tropical butterflies in north-eastern Australia. *Evol. Ecol.* 16: 399–413.
- BRABY, M. 2004. The complete field guide to Butterflies of Australia. CSIRO, Collingwood, Australia.
- BRABY, M., AND R. JONES. 1994. Effect of temperature and hostplants on survival, development and body size in three tropical Satyrine butterflies from north-eastern Australia. *Aust. J. Zool.* 42: 195–213.
- CAI, W., S. BORLACE, M. LENGAINNE, P. VAN RENSCHE, M. COLLINS, G. VECCHI, A. TIMMERMANN, A. SANTOSO, M. J. MCPHADEN, L. WU, M. H. ENGLAND, G. WANG, E. GUILYARDI, AND F-F. JIN. 2014. Increasing

- frequency of extreme El Niño events due to greenhouse warming. *Nat. Clim. Chang* 4: 111–116.
- CAI, W., G. WANG, A. SANTOSO, M. J. MCPHADEN, L. WU, F.-F. JIN, A. TIMMERMANN, M. COLLINS, G. VECCHI, AND M. LENGAGNE. 2015. Increased frequency of extreme La Niña events under greenhouse warming. *Nat. Clim. Chang* 5: 132–137.
- CHARRETTE, N. A., D. F. R. CLEARY, AND A. Ø. MOOERS. 2006. Range-restricted, specialist Bornean butterflies are less likely to recover from ENSO-induced disturbance. *Ecology* 87: 2330–2337.
- CLEARY, D. F. R., AND A. GRILL. 2004. Butterfly response to severe ENSO-induced forest fires in Borneo. *Ecol. Entomol.* 29: 666–676.
- COLLINS, M., S.-I. AN, W. CAI, A. GANACHAUD, E. GUILARDI, F.-F. JIN, M. JOCHUM, M. LENGAGNE, S. POWER, A. TIMMERMANN, G. VECCHI, AND A. WITTENBERG. 2010. The impact of global warming on the tropical Pacific Ocean and El Niño. *Nat. Geosci.* 3: 391–397.
- CSIRO, and BoM. 2007. Climate change in Australia. p. 140. CSIRO, Bureau of Meteorology, Melbourne.
- DUNN, K. L., AND L. E. DUNN. 2006. K.L. Dunn & L.E. Dunn Australian butterfly database. Beaconsfield, Victoria.
- ELITH, J., C. H. GRAHAM, R. P. ANDERSON, M. DUDIK, S. FERRIER, A. GUISAN, R. J. HIJMANS, F. HUETTMANN, J. R. LEATHWICK, A. LEHMANN, J. LI, L. G. LOHMANN, B. A. LOISELLE, G. MANION, C. MORITZ, M. NAKAMURA, Y. NAKAZAWA, J. MCCOVERTON, A. T. PETERSON, S. J. PHILLIPS, K. RICHARDSON, R. SCACHETTI-PEREIRA, R. E. SCHAPIRE, J. SOBERON, S. WILLIAMS, M. S. WISZ, AND N. E. ZIMMERMANN. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129–151.
- ELITH, J., S. J. PHILLIPS, T. HASTIE, M. DUDIK, Y. E. CHEE, AND C. J. YATES. 2011. A statistical explanation for MaxEnt for ecologists. *Divers. Distrib.* 17: 43–57.
- FISCHER, K., A. BOT, B. ZWAAN, AND P. BRAKEFIELD. 2004. Genetic and environmental sources of egg size variation in the butterfly *Bicyclus anynana*. *Heredity* 92: 163–169.
- HEWITT, J. E., AND S. F. THRUSH. 2009. Reconciling the influence of global climate phenomena on macrofaunal temporal dynamics at a variety of spatial scales. *Glob. Change Biol.* 15: 1911–1929.
- HIJMANS, R. J., S. PHILLIPS, J. LEATHWICK, AND J. ELITH. 2011. dismo: Species distribution modeling. <http://CRAN.R-project.org/package=dismo>.
- HOFFMANN, A. A., AND C. M. SGRO. 2011. Climate change and evolutionary adaptation. *Nature* 470: 479–485.
- HOLMGREN, M., C. R. DICKMAN, C. GRACIA, S. GRAHAM, J. R. GUTIERREZ, C. HICE, F. JAKSIC, D. A. KELT, M. LETNIC, M. LIMA, B. C. LOPEZ, P. L. MESERVE, W. B. MILSTEAD, G. A. POLIS, M. A. PREVITALI, M. RICHTER, S. SABATE, AND F. A. SQUEO. 2006. A synthesis of ENSO effects on drylands in Australia, North America and South America. *Advanc. Geosci.* 6: 69–72.
- HOLMGREN, M., M. SCHEFFER, E. EZCURRA, J. R. GUTIERREZ, AND G. M. J. MOHREN. 2001. El Niño effects on the dynamics of terrestrial ecosystems. *Trends Ecol. Evol.* 16: 89–94.
- HUGHES, L. 2011. Climate change and Australia: Key vulnerable regions. *Reg. Environ. Change* 11(Suppl. 1): S189–S195.
- JONES, R. 1987. Reproductive strategies for the seasonal tropics. *Insect Sci. Its Appl.* 8: 515–521.
- JONES, R., AND J. RIENKS. 1987. Reproductive seasonality in the tropical genus *Eurema* (Lepidoptera: Pieridae). *Biotropica* 19: 7–16.
- JONES, D. A., W. WANG, AND R. FAWCETT. 2009. High-quality spatial climate data-sets for Australia. *Aust. Meteorol. Mag.* 58: 233–248.
- KEARNEY, M. R., N. J. BRISCOE, D. J. KAROLY, W. P. PORTER, M. NORGATE, AND P. SUNNUCKS. 2010. Early emergence in a butterfly causally linked to anthropogenic warming. *Biol. Lett.* 6: 674–677.
- KEMP, D. J. 2001. Reproductive seasonality in the tropical butterfly *Hypolimnas bolina* (Lepidoptera: Nymphalidae) in northern Australia. *J. Trop. Ecol.* 17: 483–494.
- LATIE, M., AND N. S. KEENLYSIDE. 2009. El Niño/Southern Oscillation response to global warming. *Proc. Natl. Acad. Sci. USA* 106: 20578–20583.
- LEGENDRE, L., AND P. LEGENDRE. 1998. Numerical ecology. Elsevier, Amsterdam.
- MERRYFIELD, W. J. 2006. Changes to ENSO under CO₂ doubling in a multi-model ensemble. *J. Clim.* 19: 4009–4027.
- OKSANEN, J., F. G. BLANCHET, R. KINDT, P. LEGENDRE, P. R. MUNCHIN, R. B. O'HARA, G. L. SIMPSON, P. SOLYMOY, M. H. H. STEVENS, AND H. WAGNER. 2013. vegan – Community Ecology Package. <http://vegan.r-forge.r-project.org/>.
- PARITSIS, J., AND T. T. VEULEN. 2011. Dendroecological analysis of defoliator outbreaks on *Nothofagus pumilio* and their relation to climate variability in the Patagonian Andes. *Glob. Change Biol.* 17: 239–253.
- PATRA, P. K., S. MAKSUYTOV, AND T. NAKAZAWA. 2005. Analysis of atmospheric CO₂ growth rates at Mauna Loa using CO₂ fluxes derived from an inverse model. *Tellus* 57B: 357–365.
- PHILLIPS, S., R. ANDERSON, AND R. SCHAPIRE. 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190: 231–259.
- PHILLIPS, S., AND M. DUDIK. 2008. Modeling of species distributions with MaxEnt: New extensions and a comprehensive evaluation. *Ecography* 31: 161–175.
- PIELOOR, M. J., AND J. E. SEYMOUR. 2001. Factors affecting adult diapause initiation in the tropical butterfly *Hypolimnas bolina* L. (Lepidoptera: Nymphalidae). *Aust. J. Entomol.* 40: 376–379.
- POTTER, C., S. BORIAH, M. STEINBACH, V. KUMAR, AND S. KLOOSTER. 2008. Terrestrial vegetation dynamics and global climate controls. *Clim. Dyn.* 31: 67–78.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- ROBERTS, D. W. 2013. labdsv. <http://CRAN.R-project.org/package=dismo>.
- SRYGLEY, R. B., R. DUDLEY, E. G. OLIVEIRA, R. AIZPRUA, N. Z. PELAEZ, AND A. RIVEROS. 2010. El Niño and dry season rainfall influence hostplant phenology and an annual butterfly migration from neotropical wet to dry forests. *Glob. Change Biol.* 16: 936–945.
- SRYGLEY, R. B., R. DUDLEY, E. G. OLIVEIRA, AND A. J. RIVEROS. 2014. El Niño, host plant growth, and migratory butterfly abundance in a changing climate. *Biotropica* 46: 90–97.
- TOTH, L. T., R. B. ARONSON, S. V. VOLLMER, J. W. HOBBS, D. H. URREGO, H. CHENG, I. C. ENOCHS, D. J. COMBOSCH, R. van WOESIK, AND I. G. MACINTYRE. 2012. ENSO drove 2500-year collapse of Eastern Pacific coral reefs. *Science* 337: 81–84.
- TRENBERTH, K. E. 1984. Signal versus noise in the Southern Oscillation. *Mon. Weather Rev.* 112: 326–332.
- VANDENBOSCH, R. 2003. Fluctuations of *Vanessa cardui* butterfly abundance with El Niño and Pacific Decadal Oscillation climatic variables. *Glob. Change Biol.* 9: 785–790.
- VECCHI, G. A., AND B. J. SODEN. 2007. Global warming and the weakening of the tropical circulation. *J. Clim.* 20: 4316–4340.
- VECCHI, G. A., AND A. T. WITTENBERG. 2010. El Niño and our future climate: Where do we stand? *WIREs Clim. Change* 1: 260–270.
- WAITE, T. A., L. G. CAMPBELL, A. K. CHHANGANI, AND P. ROBBINS. 2007. La Niña's signature: Synchronous decline of the mammal community in a 'protected' area in India. *Divers. Distrib.* 13: 752–760.
- WARA, M. W., A. C. RAVELO, AND M. L. DELANEY. 2005. Climate change: Permanent El Niño-like conditions during the Pliocene warm period. *Science* 309: 758–761.
- WARREN, D. E., R. E. GLOR, AND M. TURELLI. 2010. ENMTools: A toolbox for comparative studies of environmental niche models. *Ecography* 33: 607–611.
- WILSON, P. D. 2011. Distance-based methods for the analysis of maps produced by species distribution models. *Methods Ecol. Evol.* 2: 623–633.
- WOODWARD, F. I., M. R. LOMAS, AND T. QUAIFFE. 2008. Global responses to terrestrial productivity of contemporary climatic oscillations. *Philos. Transact. Royal Soc. London B* 363: 2779–2785.